THE DIGESTIVE SYSTEM OF THE HOLOTHURIAN, CUCUMARIA ELONGATA. I. STRUCTURE OF THE GUT AND HEMAL SYSTEM

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The structure and function of the echinoderm digestive system have been the subjects of several recent papers. Anderson (1953, 1959) has made valuable contributions to the study of digestion in asteroids, and both Stott (1955) and Fuji (1961) have studied the structural and functional aspects of the echinoid gut by means of histological and histochemical techniques. As early as 1883 Hamann gave detailed accounts of the gut histology of the holothurians, *Leptosynapta* and *Holothuria*, and more recently Stott (1957) has studied the alimentary canal and associated structures in *Holothuria forskali*. Choe (1962) has given an account of gut structure and digestive enzymes found in *Stichopus japonicus*, and the feeding and digestive processes of this holothurian have been studied by Tanaka (1958). However, the process of digestion in holothurians is still not fully understood. The function of the hemal system is open to controversy, and the role of the amoebocytes in digestion has yet to be conclusively demonstrated. To provide a fuller understanding of the process of digestion it is necessary for further detailed histological and histochemical studies to be accompanied by the results of physiological studies. This paper forms an introduction to the study of digestion in *Cucumaria elongata*, and deals with the histology and histochemistry of the gut. It is intended that a second paper will deal with the distribution of the digestive enzymes.

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Material and Methods

Specimens of *Cucumaria* were collected off the Northumberland coast from depths of about 20 fathoms. Those animals required for histological and histochemical studies were treated with a suitable fixative on the day of capture.

The different gut regions were dissected out in sea water and fixed in a suitable fluid. The material was processed and embedded according to the nature of the histological and histochemical techniques to be applied. (1) For general cell structure, tissues were fixed in Heidenhain's "Susa" made with sea water, embedded in paraffin wax and sectioned at 6 μ. For finer histological structure and the identification of secretory granules, tissues were fixed in Zenker-formol. (2) For the demonstration of mucin and similar compounds (acid polysaccharides), tissues

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fixed in Heidenhain's "Susa" were stained in dilute aqueous solutions of aluminum-methylene blue (Heath, 1962), alcian blue at pH 3, and mucicarmine. To demonstrate the metachromatic staining of acid polysaccharide elements, sections were stained overnight in dilute aqueous solutions of toluidine blue (0.01%). The pH at which the acid mucopolysaccharide lost the ability to bind with methylene blue (methylene blue extinction, M. B. E.) was determined by staining sections overnight in dilute solutions (0.01%) of aqueous methylene blue at different pH values. In all cases staining was followed by rapid dehydration in 95% and absolute alcohol. (3) For general recognition of lipid deposits tissues were fixed in Baker's formol-calcium, soaked in 5% potassium dichromate for 24 hours at 60° C., embedded in gelatine, sectioned at 10–15 μ on a freezing microtome, and stained with Sudan black. For the detection of phospholipid, material was fixed in Baker's formol-calcium and treated by Baker's acid-hematin method accompanied by the pyridine extraction test applied to sections fixed in weak Bouin's fluid (Baker, 1946). Material fixed in Baker's formol-calcium, post chromed, embedded in gelatine and sectioned as above, was stained in 1% aqueous Nile blue at 60° C. and differentiated in 1% acetic acid for the demonstration of acidic lipids (Cain, 1947). (4) For the demonstration of glycogen and related compounds, material was fixed in a weak Bouin's fluid, paraffin-embedded, and sections exposed to the periodic acid-Schiff reaction. Control slides exposed to the action of 1% malt diastase in a phosphate buffer at neutrality differentiate between glycogen and other Schiff-positive substances. (5) Identification of proteins. A full account of methods for the identification of proteins is given by Pearse (1960) in Appendix 5, page 791.

(i) Identification of protein. Mercury-bromphenol blue method. (Formalin-fixed, paraffin-embedded.)
(ii) Identification of tyrosine. Millon reaction. (Baker modification).
(iii) Protein-bound NH_2. Ninhydrin-Schiff method. (Fixative: 85% ethanol. Paraffin sections.)
(iv) Identification of tryptophan.
  (a) Dimethylaminobenzaldehyde (D. M. A. B.) nitrate method. (Formalin-fixed, paraffin sections.)
  (b) Naphthyl ethylenediamine method: (Formalin-fixed, paraffin sections.) A stronger color was produced by this method than by the D.M.A.B. method.
(v) Identification of arginine. Sakaguchi reaction. (Susa-fixed, paraffin sections.)

Gut Nomenclature and Morphology

There is confusion between the present systems of nomenclature used for the holothurian gut, primarily because of the morphological variation between species, and because the names of the different gut regions appear to have been assigned by analogy with the mammalian gut, rather than being based on functional differentiation. Stott (1957) has listed the nomenclatures used by Oomen (1926), Cuénot (1948) and Stott (1957). Choe (1962) has given a nomenclature for the gut of *Stichopus japonicus,* yet none of these is suitable for the gut of *Cucumaria.*

The system of nomenclature used throughout this study is as follows: pharynx, esophagus, stomach, constriction, intestine I, intestine II and cloaca. Each of these regions is morphologically clearly differentiated from the others (Fig. 1). By using terms which are familiar in the description of mammalian digestive systems, it is not intended that any functional comparisons should be drawn. Such names are retained only until a nomenclature based on functional differentiation can be given.

The first region of the gut, the *pharynx,* lies in the center of the aquapharyngeal bulb, and upon emergence into the body cavity it takes the form of the *esophagus.* The esophagus is slender yet conspicuous, having patches of black pigmentation at its anterior end. It is followed by a much broader and thicker-walled *stomach,* which is usually of similar length, but its pink coloration contrasts with the grey color of the esophagus. Following the stomach is a short, thin-walled region,

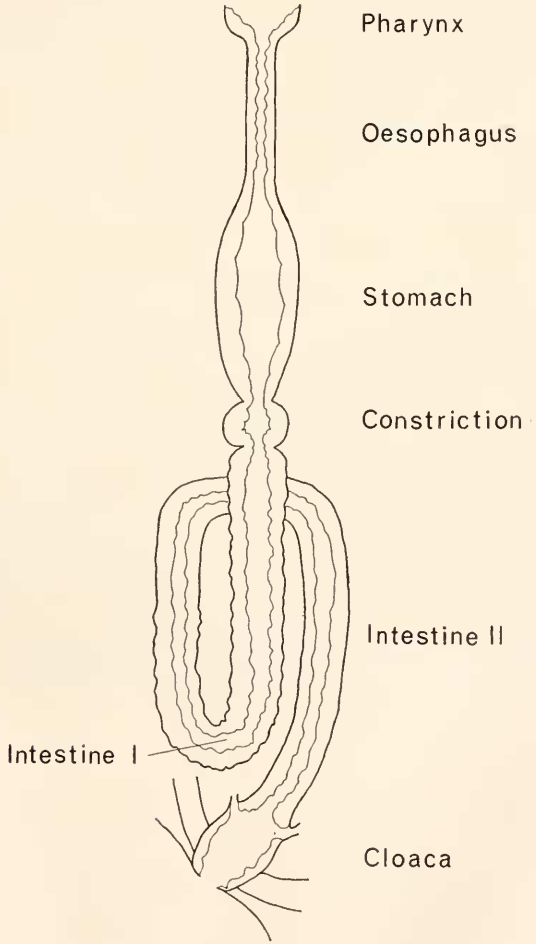
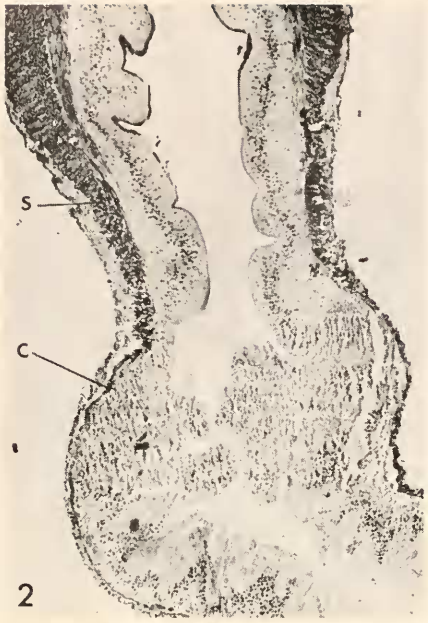
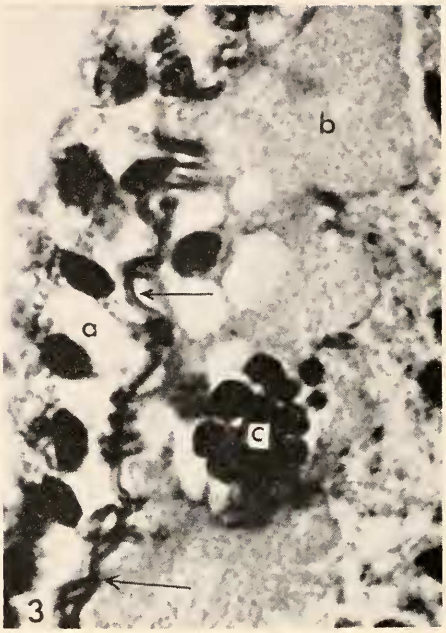


FIGURE 1. The gut of *Cucumaria elongata.* For details of gut nomenclature see text.





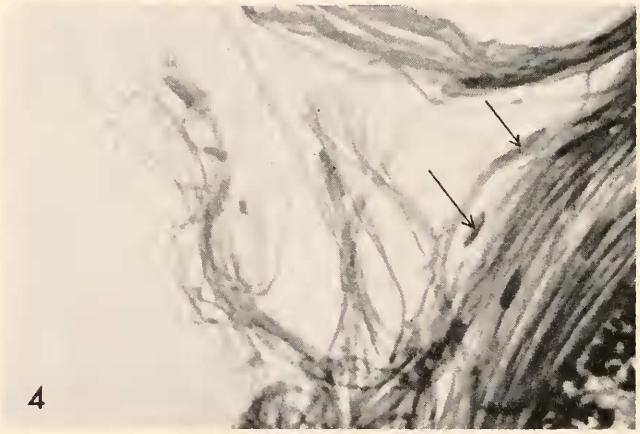


FIGURE 2. Longitudinal section through the junction between stomach and constriction. Compare the development of circular muscle in the stomach (S) with that in the constriction (C). Masson's trichrome. 1 cm. = 100 μ.

FIGURE 3. Transverse section of intestine I, showing muscle cell bodies (a), muscle layer (indicated by arrows), and connective tissue-fluid complex (b). C is an amoebocyte held in the fluid complex. Masson's trichrome. 1 cm. = 10 μ.

FIGURE 4. Circular muscle fibers of the stomach teased to show muscle cell bodies (indicated by arrows). Masson's trichrome. 1 cm. = 20 μ.

approximately 2–3 mm. long, which is bounded anteriorly and posteriorly by pronounced constrictions. Throughout this study this region of the gut is known as the *constriction.* The green color of the constriction contrasts vividly with the brown of the intestine and the pink of the stomach. The intestine of *Cucumaria* is typical of holothurians in being very long. *Intestine I* is about half as long again as *intestine II.* There is no color difference between these two parts, but the change from I to II is made clear by the change from the convoluted gut wall of intestine I to the relatively smooth-walled intestine II. The right and left respiratory trees open into the most posterior part of intestine II, from which point the gut is known as the *cloaca.* The *cloaca* is relatively short and runs to the posterior extremity of the animal.

Structure of the Gut

The gut wall consists of a number of distinct layers which can be described as follows:

(a) An outer covering of ciliated serosal epithelium which in places is so thin that it can only be detected by the presence of its nuclei.

(b) To the inside of the ciliated epithelium is a distinct layer of cells which are thought to be the cell bodies of the circular muscle fibers which lie to the inside of them.

(c) A muscle layer which is variously represented in the different regions of the gut. Outer circular and inner longitudinal muscle fibers are present in all gut regions. In the stomach the muscle bands show their maximum development, and are chiefly responsible for the thickness of the gut wall. At the junction between the stomach and the constriction there is a marked change in the musculature of the gut (Fig. 2). In the constriction the circular muscle is reduced to a band of fibers about 4 μ wide, while the longitudinal muscle is present as a few scattered fibers. This condition persists throughout the intestine and cloaca.

(d) A connective tissue layer, associated with which is a fluid continuous with that in the hemal system. The fluid component is variously represented in the different regions of the gut and is described fully below.

(e) The mucosal epithelium which, except in the stomach, is chiefly responsible for the thickness of the gut wall. It is composed of a single layer of tall slender cells, among which are several cell types described fully below.

Muscle cell bodies

A distinct layer of cells, varying from 10 to 15 μ thick and lying to the outside of the circular muscle (Fig. 3), is thought to comprise the cell bodies of the circular muscle fibers. The layer is present in all gut regions, and is covered by the serosal epithelium. In stained preparations cut both transversely and longitudinally it is difficult to interpret the relationship between the cell bodies and the fibers since both are densely packed. Even when pieces of the gut wall are teased and then stained with Masson's trichrome, the relationship is still obscure. There is no indication that these areas might be fiber bundles of a nerve layer, and the original contention that these cells are muscle cell bodies is held in view of the following observations. Preparations of esophagus, constriction and intestine, cut

transversely and stained in Masson's trichrome, failed to show muscle cell bodies lying along the length of the circular fibers. In all the above regions the circular muscle fibers form a narrow layer, approximately 12–15 μ wide in the esophagus, compared with the thickness of a few fibers in the other regions. In these regions the muscle cell bodies must lie to the outside of the fibers. The cell bodies are highly distended and must be connected to individual fibers by way of short necks. In the stomach, where the circular muscle attains a thickness of 75 μ, muscle cell bodies can be clearly seen lying along the length of many of the fibers (Fig. 4). If the innermost fibers of the stomach were to have cell bodies arranged in the manner described for other gut regions, the connection between cell body and fiber would be *via* a neck in the region of 70 μ long. The presence of a thick overlying layer of densely packed muscle fibers makes such a connection unlikely. It is suggested that only the outermost circular fibers of the stomach have this highly distended type of cell body, whereas all fibers have this arrangement in the regions where the development of circular muscle is not as extensive. Although it has

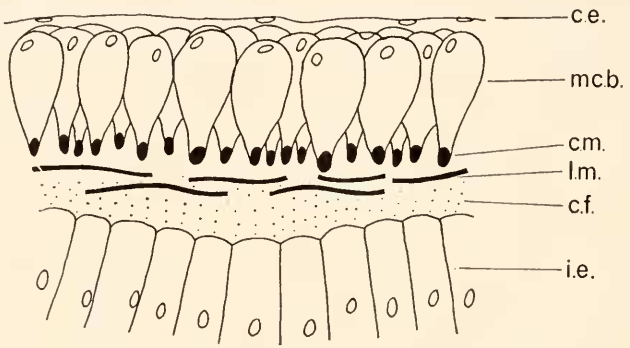


FIGURE 5. Semi-diagrammatic representation of the relationship between muscle cell bodies and the circular muscle fibers as seen in longitudinal section: c.e., coelomic epithelium; m.c.b., muscle cell bodies; c.m., circular muscle; l.m., longitudinal muscle; c.f., connective tissue-fluid complex; i.e., mucosal epithelium.

proved impossible to demonstrate conclusively that this arrangement exists, the proposed relationship between cell bodies and the individual muscle fibers is shown diagrammatically in Figure 5. Electron micrographs are necessary to give a clear picture of the arrangement which exists in this part of the gut wall.

The connective tissue-fluid complex

The connective tissue layer attains its maximum development at the bases of the villus-like projections of the esophagus where it doubtless acts as a supporting framework. The most interesting aspect of this complex is the fluid component which is continuous with the fluid of the hemal system (Fig. 6). In living preparations the hemal fluid has a viscous appearance, whilst on fixation it appears to become "gelled." Amoebocytes are present in this fluid medium (see Fig. 3). Histochemical tests indicate that the fluid is periodic acid-Schiff-positive (diastase-fast) (Fig. 7), and contains tryptophan, arginine, tyrosine and reactive NH_2 groups, together with an acid mucopolysaccharide.

The mucosal epithelium

The mucosal epithelium is composed of a single layer of tall, slender cells which have centrally placed nuclei. Cells specialized to produce currents in the lumen of the gut are absent. In the esophagus the cells are formed into villus-like projections which have a connective tissue framework, and the individual cells are interspersed with large, conspicuous mucous gland cells (Fig. 8). Histochemical tests show that the glands contain an acid mucopolysaccharide with methylene blue extinction below pH 2. Negative results were obtained with the periodic acid-Schiff technique (Table I). Only a few of the glands extend to the basement membrane of the epithelium; those which do have a swollen basal portion (6–7 μ). The majority of the mucous glands are interspersed among the distal parts of the epithelial cells, and open by way of short necks into the esophageal lumen. In fixed preparations stained in aluminum-methylene blue, the contents of the glands appear distinctly granular. In the pharynx the mucous glands are similarly distributed.

TABLE I

Histochemistry of the gland cells

Test	Esophageal glands	Constriction glands	Intestine I glands
Toluidine blue	Gamma metachromasia	Gamma metachromasia	Negative
Alcian blue, pH 3	Positive	Positive	Negative
Aluminum-methylene blue	Positive	Positive	Negative
Mucicarmine	Positive	Positive	Negative
Methylene blue extinction	Below pH 2	Below pH 2	Negative to methylene blue
Periodic acid-Schiff reagent	Negative	Negative	Negative

In the stomach the cells of the mucosal epithelium are covered by a cuticle which has a thickness of about 2 μ (see Fig. 15). Mucous glands are absent and the gland cells which have been demonstrated by Hamann (1883) in the stomachs of *Leptosynapta* and *Holothuria* are lacking in *Cucumaria*. Chains of secretory granules found in the lining epithelial cells of the stomach of *Echinus esculentus* (Stott, 1955) and *Strongylocentrotus intermedius* (Fuji, 1961) have not been demonstrated, and the most conspicuous feature of the structure of the stomach wall of *Cucumaria* is its heavy musculature.

The epithelial cells of the constriction are formed into stout villus-like projections similar to those of the esophagus, and interspersed among individual cells there are numerous mucous gland cells which invariably extend to the basement membrane of the epithelium (Fig. 9). The base of the mucous glands has a diameter (6 μ) much greater than that of the neighboring epithelial cells. These glands show histochemical reactions similar to those of the esophagus (Table I), and when stained in aluminum-methylene blue the contents appear granular. Sections of the esophagus and constriction stained in aluminum-methylene blue, made with polychrome methylene blue (Microme salt no. 1041—E. Gurr), show differences in the staining reaction of the mucous glands after the preparations have been

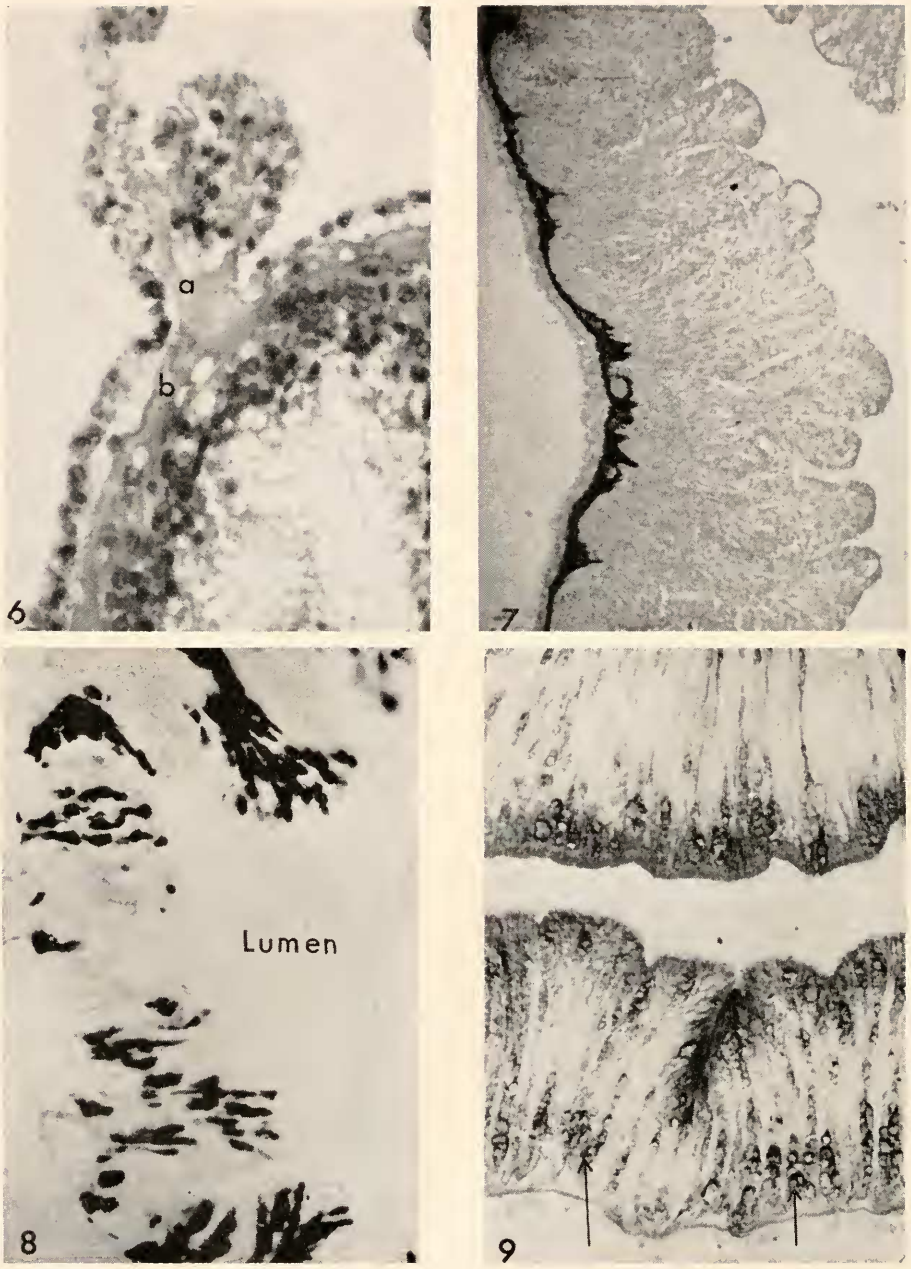


FIGURE 6. Transverse section of intestine I and the dorsal hemal sinus, showing the continuity between the hemal fluid (a), and the gut fluid complex (b). Masson's trichrome; 1 cm. = 15 μ.

FIGURE 7. Longitudinal section of intestine II, showing the fluid complex. Periodic acid-Schiff; 1 cm. = 50 μ.

stored for a few days. Mucous glands in the esophagus retain the brilliant blue-coloration characteristic of sulfated mucopolysaccharides, while those of the constriction change from blue to reddish purple. This would seem to indicate differences in the chemical nature of the secretion from these glands.

Preparations of the constriction stained in Heidenhain's iron hematoxylin and Masson's trichrome show two characteristic features. First, the swollen basal portion of the mucous glands is represented by light-colored areas in arcades between the bases of the epithelial cells. Secondly, there is a faintly stained "fringe" area, permeated by the ducts of the mucous glands, which represents the distal portion of the epithelial cells (Fig. 10). Throughout this fringe region histochemical tests show the presence of an acid mucopolysaccharide which has the same histochemical reactions as the glands of the esophagus and constriction, yet distinct gland cells are absent. Preparations stained in Heidenhain's iron hematoxylin also show secretory cells which contain chains of secretory granules (Fig. 11) similar to those described by Anderson (1953) in the pyloric caeca of *Asterias forbesi*. It has proved difficult to clearly establish the relationship between the secretory granules and the secretory cell, but in most cases the granules extend in rows towards the free end of the cell.

The organization of the epithelial cells throughout the intestine and cloaca is similar to that in the constriction, yet mucous glands and secretory granules are absent. Interspersed among the distal portions of the epithelial cells in intestine I, distinct gland cells are present which open into the lumen of the intestine (Fig. 12). These cells have only been demonstrated using Heidenhain's iron hematoxylin, and the contents appear granular. The nucleus is situated in the proximal half of the cell. Similar gland cells have been shown in the intestine of *Holothuria* by Hamann (1883). The distal portion of the epithelial cells of the intestine, corresponding to the "fringe" zone of the constriction, show faintly positive reactions for acid mucopolysaccharide. As in the "fringe" of the constriction, distinct gland cells are absent.

Storage cells

The mucosal epithelial cells in all regions of the gut hold deposits of lipid (Fig. 13), which constitutes an important food reserve of the animal (Fish, 1967). The lipid is stored in the form of droplets which lie both above and below the nucleus. In the distal region of the epithelial cells the droplets are generally small and sparsely distributed while in the basal portion they appear to have coalesced into larger globules. The Nile blue technique reveals that acidic lipids are prominent in the composition of the lipid deposits. The acid hematin test (Baker, 1946), accompanied by pyridine extraction, gave doubtful results for the presence of phospholipid. Lipid deposits are also present in the much inflated cell bodies of the circular muscular fibers. Sudan black staining shows that the muscle cell bodies are crowded with lipid droplets, the histochemistry of which is the same as that of lipid stored in the epithelial cells.

FIGURE 8. Transverse section of esophagus, showing mucous glands. Aluminum-methylene blue; 1 cm. = 35 μ.

FIGURE 9. Longitudinal section of the constriction, showing mucous glands (indicated by arrows). Aluminum-methylene blue; 1 cm. = 35 μ.

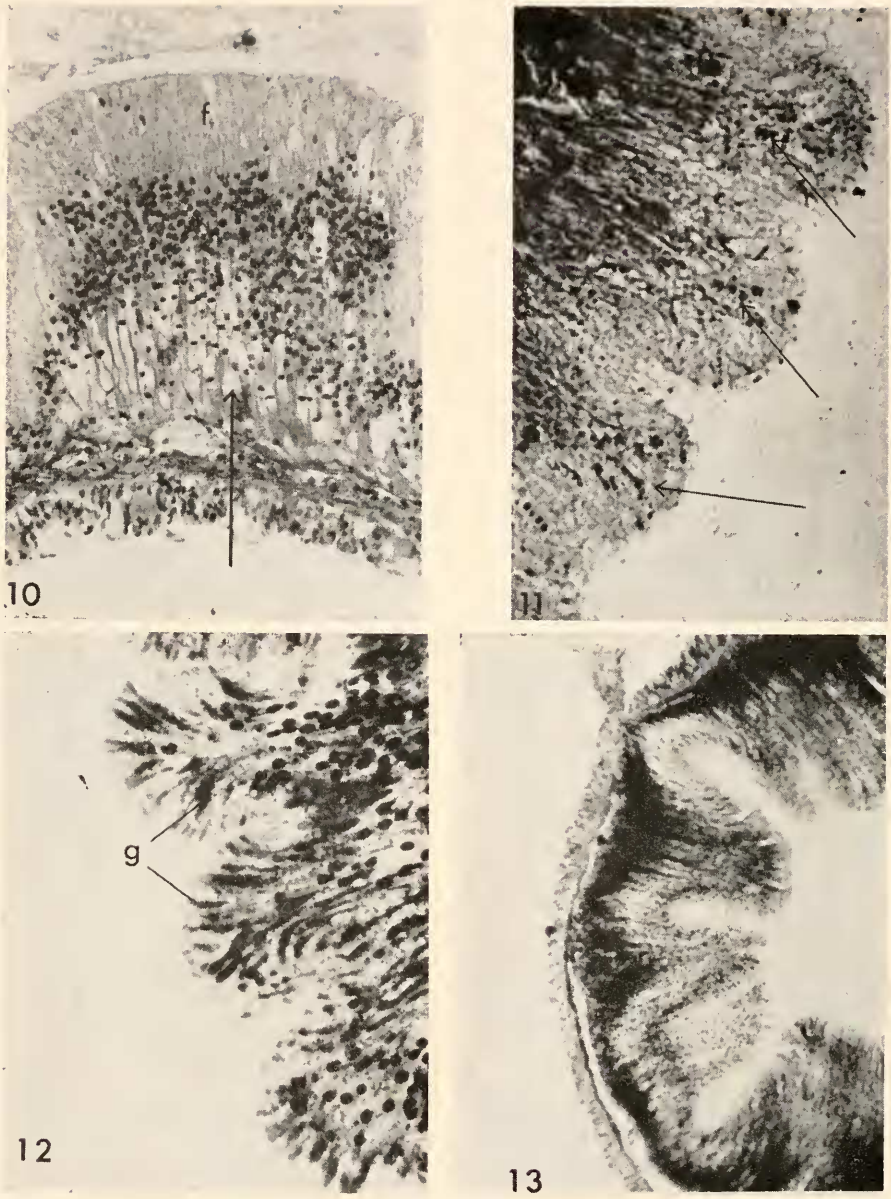


FIGURE 10. Transverse section of the constriction. Basal portion of mucous glands indicated by arrow. Note lightly stained "fringe" zone at f. Masson's trichrome; 1 cm. = 40 μ.

FIGURE 11. Transverse section of the constriction, showing chains of secretory granules. Heidenhain's iron hematoxylin; 1 cm. = 30 μ.

FIGURE 12. Longitudinal section of intestine I, showing gland cells (g). Heidenhain's iron hematoxylin; 1 cm. = 30 μ.

FIGURE 13. Transverse section of the constriction, showing lipid deposits. Note concentration of lipid in basal portion of cells. Frozen sections, Sudan black; 1 cm. = 55 μ.

The Hemal System

Typical of holothurians there is a close association between the gut and the hemal system. The system in *Cucumaria* is shown diagrammatically in Figure 14, and consists of two main sinuses—the dorsal and the ventral. There is no rete mirabile or complicated network of lacunar tufts such as is found in *Holothuria forskali* (Stott, 1957) and other large aspidochirotes, yet transverse connections between different parts of the same sinus are evident (Fig. 14). A direct route between the hemal system and the gut is provided by the continuity which exists

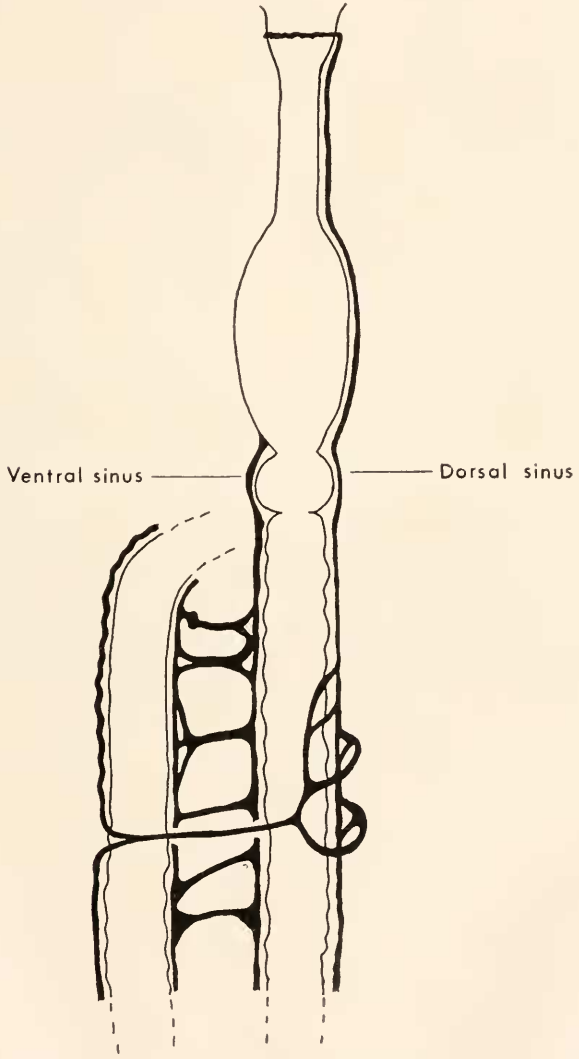


Figure 14. Hemal system of *Cucumaria,* showing dorsal and ventral sinuses and their connecting strands.

between the hemal fluid and the connective tissue-fluid complex of the gut (see Fig. 6).

The ventral sinus runs along the length of the intestine and constriction, yet at the anterior end of the constriction the sinus ceases to exist as a separate channel, and serial sections at this point show that it passes diffusely through the stomach wall until it reaches the connective tissue-fluid complex (Fig. 15). The author is not aware of a similar system in any other holothurian; the more usual arrangement is for the ventral vessel to continue along the length of the stomach and esophagus until it reaches the hemal ring surrounding the pharynx.

Throughout its course the ventral sinus is in close association with the gut wall. At the anterior region of intestine I the sinus gives off several transverse

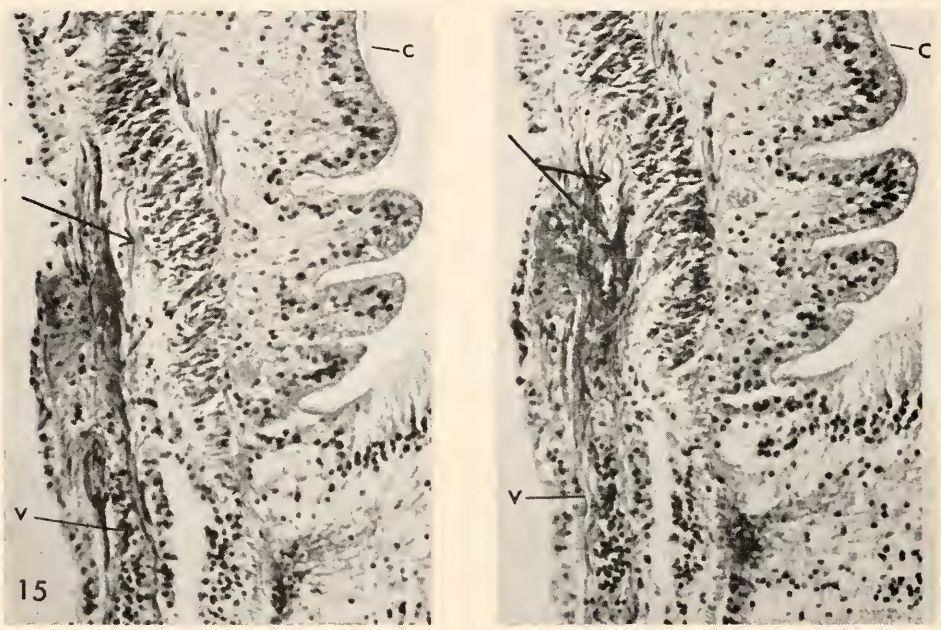
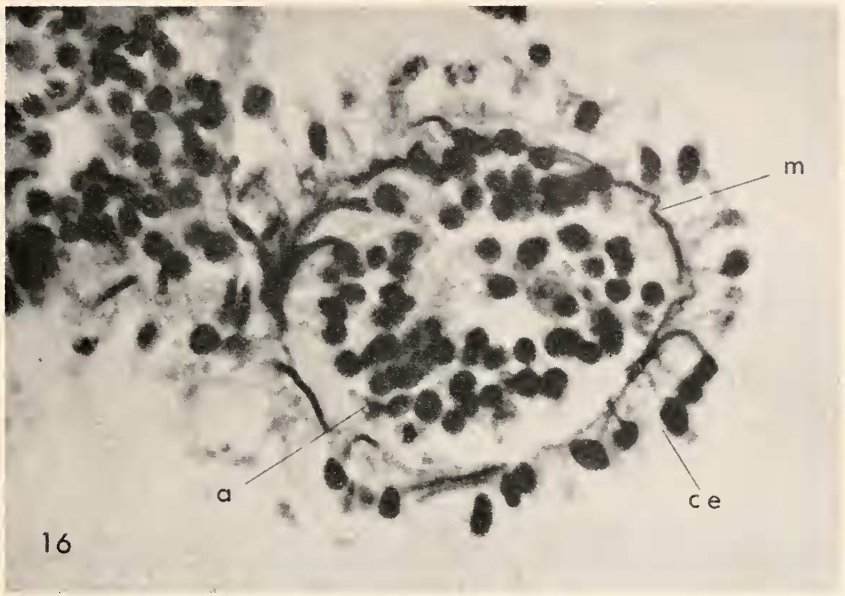


FIGURE 15. Serial longitudinal sections through the junction between stomach and constriction, showing the ventral hemal sinus (v) merging with the stomach wall at points indicated by arrows. Note the cuticle (c) covering the mucosal epithelial cells of the stomach. Masson's trichrome; 1 cm. = 40 μ.

connections which join with that part of the ventral sinus which is associated with the posterior part of intestine I and the anterior part of intestine II.

The dorsal sinus runs along the complete length of the gut on the side which is attached by the dorsal mesentery. It is connected to the intestinal wall by numerous branches, and shortly after the commencement of its course along intestine I, it gives off a single transverse connection which joins the part of the dorsal sinus which is associated with the anterior part of intestine II. Anteriorly the dorsal sinus diminishes towards the pharynx. The presence of a hemal ring has not been satisfactorily demonstrated, yet this may be due to its delicate nature and the fact that it is believed to lie directly behind the water vascular ring.



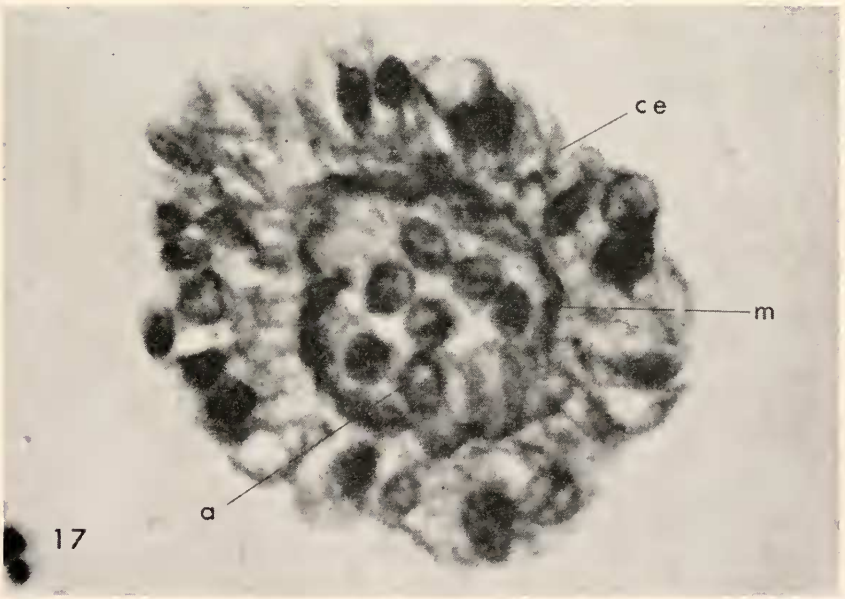


FIGURE 16. Dorsal hemal sinus seen in transverse section. Note coelomic epithelium, ce; muscle layer, m; and amoebocytes within the sinus (a). Heidenhain's iron hematoxylin, 1 cm. = 10 μ.

FIGURE 17. Transverse connecting strand of the ventral hemal sinus seen in transverse section. Note coelomic epithelium, ce; muscle layer, m; and amoebocytes within the sinus (a), Masson's trichrome; 1 cm. = 10 μ.

Although the small size and delicate nature of the hemal sinuses make it difficult to obtain good sections, available evidence suggests that all parts of the system have the same histological structure (Figs. 16 and 17). There is an outer layer of coelomic epithelium which contains strands of connective tissue. The thickness of this layer varies from 4–5 μ to 10–12 μ. A thin but distinct layer of circular muscle fibers is found to the inside of the coelomic epithelium. Associated with the circular muscle fibers there are a few scattered longitudinal fibers, to the inside of which is an indistinct layer of connective tissue. In all sections of the hemal sinuses the circular muscle fibers have shown as a distinct layer. This contrasts with *Stichopus chloronotus* (Sivickis and Domantay, 1928), which has an indistinct muscle layer in the hemal sinus. The lacunar tufts of the rete mirabile of *Actinopyga* were found by Hyman (1955) to be without a muscle layer.

Sections of the hemal sinuses treated with aluminum methylene blue and the periodic acid-Schiff technique gave negative results.

Discussion

The results of histological and histochemical observations on the gut of *C. elongata* present several interesting features. The relationship between the muscle cell bodies and the individual circular muscle fibers poses problems as to the reasons for, or advantages of, such a system. Nichols (1959) has described a similar arrangement of muscle cell bodies in the ampullae of the tube feet of *Echinocardium*. Such an arrangement has not previously been recorded in the gut wall of holothurians. The development of this system is perhaps associated with the lack of connective tissue in the outer layers of the gut wall. The layer of inflated, densely packed and interlocking muscle cell bodies may function as an anchorage system for the circular muscle fibers. In the absence of connective tissue in this region, such an arrangement would be important during phases of strong muscle contraction.

Lipid stores are held in the muscle cell bodies as well as in the cells of the mucosal epithelium. Nichols (1959) found that in *Echinocardium,* glycogen was held in the muscle cell cytoplasm as a food store. Glycogen has not been detected in either the body wall or gut of *Cucumaria*. The failure to obtain a positive Baker test for the presence of phospholipid is interesting, in that Anderson (1953) and Karnovsky *et al.* (1955) failed to demonstrate phospholipid in *Asterias*. However, as pointed out by Karnovsky *et al.*, the failure of the test may be due to the low phosphorus content of the phosphatide fraction and not due to the low concentration of phosphatide. In the acid hematin test, the hematin is presumed to react with the phosphate radical. Although the specificity of the Baker test is established (Casselman, 1952), its sensitivity has never been determined, and it may be that in spite of negative results, phospholipids are present in the constitution of the lipid deposits. It must also be emphasized that as marine invertebrates have low melting point lipids (Giese, 1966), the technique used in the histochemical localization of the lipid deposits is itself questionable, as it involved incubation in 5% potassium dichromate for 24 hours at 60° C.

Results similar to those obtained for the histochemistry of the hemal fluid in *Cucumaria* have been recorded by Millot and Vevers (1964) for the axial organ secretion in echinoids. These authors suggest that the axial organ is suitably

positioned to act as an endocrine organ, and they have shown that considerable quantities of secretion leave the glandular recesses of the organ. Millot (1966) has further suggested that the reactions of the axial organ may be part of a "defensive injury response." In holothurians there is little agreement between authors on the existence of an axial gland. Cuénot (1891) claims that the part of the coelom giving rise to the axial gland disappears during embryonic development, while other workers described a connective tissue network to the side of the water ring which they considered to be an axial gland (*vide* Hyman, 1955). It is significant to note that even though the axial organ in echinoids may secrete fluid into the hemal system, Millot and Vevers (1964) believed it unlikely that amoebocytes arose there. Furthermore, Holland *et al.* (1965) were unable to find evidence either for or against the participation of the axial organ in amoebocyte production.

Although the structure and possible functions of the hemal system have been investigated by a number of authors, the functions of the system have not been conclusively demonstrated. A number of investigators have reported a contractile nature for parts of the hemal system (Kawamoto, 1927; Prosser and Judson, 1952; Boolootian and Campbell, 1964; see also Hyman, 1955). Prosser and Judson (1952) further demonstrated that in holothurians the contractions were myogenic, being accelerated by adrenalin and slowed by atropin. Burton (1964) has shown that despite evidence of contractility of the sinus in regular echinoids, the full significance of this is not yet clear, and it would appear unlikely that the hemal system functions as a true circulatory system. The experiments and histological observations of Enriques (1902), Oomen (1926), and Schreiber (1930, 1932a, 1932b), led to the hypothesis that the holothurian hemal system played an important role in digestion, in that amoebocytes contained within the hemal fluid were believed to carry digestive enzymes into the gut, and carry away the products of digestion. Contrary to these earlier reports it has recently been suggested that sugars may cross the gut wall by active transport (D'Agostino and Farmanfarmaian, 1960; Rundles and Farmanfarmaian, 1964). It has further been shown that the hemal sinuses are not significantly involved in nutrient transport in either echinoids or holothurians (Farmanfarmaian and Phillips, 1962; Farmanfarmaian, 1963). Results of histochemical tests applied to sections of gut material of *Cucumaria* are also contrary to the hypothesis of Enriques, Oomen and Schreiber. These results show that parts of the mucosal epithelium of the gut appear to be capable of secreting digestive enzymes. The constriction has abundant mucous glands and chains of secretory granules, and intestine I has conspicuous gland cells. The distribution of mucous glands, secretory granules and gland cells would appear to indicate that at least the constriction and intestine I are sites of enzyme production and secretion. The possibility of ascribing a zymogenic function to parts of the lining epithelium of the gut will be considered more closely in the second part of this study when the results of the distribution of digestive enzymes are discussed.

Summary

1. A system of nomenclature is given for the gut of *Cucumaria elongata*. The different regions of the gut have been named as follows: pharynx, esophagus, stomach, constriction, intestine I, intestine II, and cloaca.

2. The gut wall is composed of five distinct layers: (a) an outer serosal epithelium; (b) muscle cell bodies of the circular muscle fibers; (c) a muscle layer with outer circular and inner longitudinal fibers; (d) a connective tissue-fluid complex, the fluid component of which is continuous with the fluid in the hemal system; (e) the mucosal epithelium, which is composed of a single layer of tall slender cells.

3. Interspersed among the cells of the mucosal epithelium are mucous glands, secretory granules and gland cells. Mucous glands are present in the esophagus and constriction; secretory granules in the constriction, and gland cells in intestine I. Cells specialized to produce currents in the lumen of the gut are absent.

4. Stores of lipid are held in the cells of the mucosal epithelium and in the muscle cell bodies of the circular muscle fibers. Glycogen deposits have not been demonstrated.

5. The histology of the hemal system has been studied and the role of the hemal system in digestion is discussed.

6. From the distribution of gland cells and secretory granules it is suggested that the mucosal epithelial cells of the constriction and intestine I are sites of digestive enzyme production and secretion.

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